

QL

468

A5

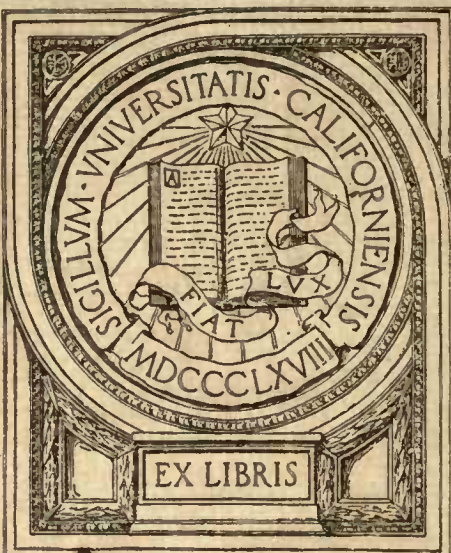
UC-NRLF



C 2 741 499

QL 468
A5

EXCHANGE



EX LIBRIS

Main Lib. Zoology Dept.

BIOLOGY
LIBRARY
G

SMITHSONIAN CONTRIBUTIONS TO KNOWLEDGE.

THE

CLASSIFICATION OF INSECTS

FROM

EMBRYOLOGICAL DATA.

By PROF. LOUIS AGASSIZ.
"

[Presented to the American Association for the Advancement of Science, at Cambridge, August, 1849.]

[RECEIVED, MARCH 6, 1850.]

VOL. II.

ART. 6.
UNIVERSITY OF CALIFORNIA

QL 468
A 5
BIOLOGY
LIBRARY
G

COMMISSION

TO WHICH THIS MEMOIR HAS BEEN REFERRED.

PROF. C. D. MEIGS.

THADDEUS W. HARRIS, M. D.

JOSEPH HENRY, *Secretary.*

Main Lib, Zool. Dept

CAMBRIDGE:
METCALF AND COMPANY,
PRINTERS TO THE UNIVERSITY.

THE
CLASSIFICATION OF INSECTS

FROM
EMBRYOLOGICAL DATA.

I. GENERAL CONSIDERATIONS.

THE various classifications of Insects which have been proposed by zoölogists rest either on considerations derived from their external characters and form, and in part from their internal structure, or on the various modes of their development from the egg. The earliest writers on classification availed themselves principally of the number and structure of their wings, to divide the numberless insects into several general divisions, and such an arrangement, as finally adopted by Linnæus, has prevailed to a great extent, sometimes modified by the introduction of some smaller groups, which have been more generally admitted by English writers than by those of the Continent of Europe.

Fabricius introduced an entirely new view of the subject, dividing the insects according to the structure of the organs by which they take their food, and the various structures and degrees of complication of the jaws became the foundation of his system, which he not only applied in a general manner, but worked out in all its details, assigning even to the smaller divisions characters derived chiefly from the peculiar form of those parts.

More recently the metamorphosis of insects has been made the foundation of their classification, and they have been grouped according to the extent of the changes they undergo from the egg, and according to the condition in which the young animal remains for a time before it has arrived at its complete perfect growth.

According to these views, those insects that are hatched from the egg with a form very similar to the full-grown perfect animal, and which undergo slight or only partial changes during their growth, such as the additional development of wings, or which remain active throughout their metamorphosis, have generally been considered as belonging to one and the same great division, and have been brought together as insects without metamorphosis, or with imperfect metamorphosis. On the other hand, such insects as are hatched from the egg in the form of a maggot,

grub, or caterpillar, resembling worms in their earlier period of life more than they resemble the perfect insects which are to grow out of them, and from that condition passing into the state of immovable, mummy-like pupæ, or chrysalids, and during this period taking no food, but afterwards giving rise to a winged, perfect fly, beetle, or butterfly, have been considered as insects with perfect metamorphoses, and on that account have been brought together in one great division.

A glance at the classifications resting upon such considerations will show, that each of these fundamental divisions contains insects, which, in their perfect condition, chew their food with powerful jaws, and others which are provided with suckers to pump the more liquid nourishment upon which they live. It has long been a question with me, whether the nature of the metamorphoses or the structure of the jaws was to be considered as the prominent character on which to found the primary divisions. It struck me as possible, that a classification, in which the chewing insects should be brought together, and all sucking insects combined in another group, and both then subdivided according to their transformations, might lead to as natural an arrangement as a classification resting in its fundamental divisions upon considerations derived from the metamorphoses alone. In order to satisfy myself upon the importance of these two sets of characters, I have examined the metamorphoses themselves, which various groups of insects undergo, and have been deeply impressed with the fact, that most of those insects which undergo the so-called complete metamorphoses are provided, in their early stages of growth, with a chewing apparatus, which is gradually transformed into the various kinds of suckers with which the perfect insects are provided.

This led me to the question, whether the structure of this peculiar apparatus for chewing food did not indicate, among insects, a condition of existence lower than that of those insects which assume during their metamorphosis another type of jaws in the shape of a sucker. And upon that suggestion I attempted an arrangement of the different orders of insects, which seems to me not only more natural, but to correspond more fully with the lessons of embryology. I propose the following classification: —

I. *Chewing Insects* (Mandibulata).

NEUROPTERA,
COLEOPTERA,
ORTHOPTERA,
HYMENOPTERA.

II. *Sucking Insects* (Haustellata).

HEMIPTERA,
DIPTERA,
LEPIDOPTERA.

The reason why Coleoptera have been so universally considered as the highest among insects, is plainly shown by the position assigned to *Cicindela*, which is placed at the head. That group is the most carnivorous of the order. But I do not think it right to assign to the carnivorous insects the highest rank, if there is no other reason to consider them as such than the fact, that among Mammalia the Carnivora rank higher than the herbivorous animals.

Far from inclining to such views, I am prepared to show that the very fact of the complication of their jaws, and the multiplication of their parts, the greater resemblance which those parts have to common legs, the immobility of the prothorax, the hardness of their anterior wings, the frequent deficiency of the lower wings, the similarity in structure between the jaws of the larva and those of the perfect insect, are so many characters which assign to the Coleoptera a lower rank than that of the Lepidoptera.

Indeed, if we institute a comparison between Coleoptera and Lepidoptera, we are struck with the greater resemblance between the former, when perfect, and the caterpillar, than between the beetle and the butterfly. It may be said, that the beetle preserves the characters of the larvæ of other insects, and assumes only wings and more developed legs in addition, without reaching other successive metamorphoses, — those other changes through which the caterpillar passes before it is transformed into the perfect imago.

This being once granted, it must be acknowledged, in general, that chewing insects should rank lower than sucking insects; and we may perhaps find in the complete metamorphoses of the higher *Haustellata* sufficient data to carry out this view in determining the relative position to be assigned to all the orders of that class.

Among the mandibulate insects, for instance, we have, besides Coleoptera, the Orthoptera, Neuroptera, and Hymenoptera. Now, the Neuroptera, though undergoing metamorphoses as complete, in many respects, as the Coleoptera, have larvæ whose structure seems decidedly lower than that of the Coleoptera, for they are mostly aquatic worms, provided not only with powerful jaws and all the complicated chewing apparatus of mandibulate insects, but also with aquatic respiratory organs, namely, true external gills similar to those of the aquatic worms. And the great and complicated changes which they undergo, both in structure and form, lead to a development which does not rank higher than that observed among Coleoptera. Indeed, the soft wings of Neuroptera indicate, in my opinion, a character of low development; for their peculiar structure resembles more that of the wings of the young butterfly, before passing into the condition of the pupa, than that of the elytra. The wings of Coleoptera, again, resemble more closely the condition of the wings in the pupa of the butterfly, at the period when the outer wing is hardened and soldered to the body, covering the lower wings, which remain soft. I would, therefore, without hesitation, place Neuroptera as the lowest order among Mandibulata.

Next might come the Coleoptera, followed by the Orthoptera; for Hymenoptera, no doubt, rank highest in this division. To satisfy ourselves that this is the case, we need only consider the structure of their jaws, the upper pair of which alone preserve the character of chewing insects, while the lower are transformed into a kind of proboscis very similar to that of *Haustellata*. Again, their larvæ rank higher than the larvæ of either Neuroptera or Coleoptera. They are for the most part larvæ with aerial respiratory organs, and, in that respect, rank decidedly above those of Neuroptera, and might be considered as of equal value with those of Coleoptera.

Though the fact, that many Hymenoptera have caterpillar-like larvæ, will at once place them one stage higher, that is, nearer the Haustellata, some facts presently to be mentioned, respecting the changes which caterpillars undergo before they pass into the state of complete pupæ, will establish more fully the value of this argument.

There is, however, one order of chewing insects, the position of which is somewhat embarrassing; I mean the Orthoptera. If the views expressed above are correct, the very fact of their having chewing jaws will place them among the Mandibulata, below the Haustellata. But what is the proper position to assign to them among Mandibulata? They cannot be placed higher than the Hymenoptera, for their jaws are completely masticatory. But their position in relation to Coleoptera and Neuroptera is difficult to determine. They undergo no change after they have been hatched from the egg, except that of assuming wings. They are born from the egg with an aerial respiratory system; indeed, in a condition which is already higher than that of the larvæ of Coleoptera, and decidedly higher than that of the Neuroptera. We should, therefore, look to the changes which these animals undergo within the egg, to determine their true position. But upon this point observations are still wanting. At present I am inclined to place them above Coleoptera, as we generally find that the degree of perfection which the young assumes before it is hatched corresponds, to a remarkable extent, with the perfection of the animal in its general structure. And if it were not for the peculiar structure of the jaws in Hymenoptera, I should not hesitate to place Orthoptera highest among Mandibulata. Again, the perfection of the wings of Hymenoptera leads so decidedly to a parallelism between them and some of the moths, that I cannot help thinking the best arrangement is the one mentioned above; namely, Neuroptera lowest, next Coleoptera, next Orthoptera, and Hymenoptera highest. The peculiar piercers, with which so many Orthoptera are provided to lay their eggs, remind us of similar apparatus in Hymenoptera, which would go to substantiate the position now assigned to these two orders of insects, in close juxtaposition.

Let us now consider the different orders belonging to the division of the Haustellata, which contains only three great groups, the Hemiptera, Diptera, and Lepidoptera. The order in which I have mentioned them above seems to me to be that in which they should naturally be placed, according to their structure and metamorphoses. If we can be guided by the changes which the highest of these animals undergo, it will be perceived that among Lepidoptera we have the true key for their natural arrangement. The larvæ of this last group are hatched in a condition far superior to that of the larvæ of any other insects. Not only are they all provided with aerial respiratory organs, but the different regions of their body are already more fully marked out than in the larvæ of any other insects, by the different structure of their various legs, and by the decided distinction which is introduced between the head and body. Moreover, their skin is variously colored, and provided with a most astonishing diversity of external appendages.

At first, these animals are voracious in their habits. Provided with powerful jaws, they chew large quantities of food, mostly derived from the vegetable kingdom.

But before they undergo their metamorphosis into pupæ, before casting the last skin of the caterpillar, the young *Lepidoptera* begin to form their wings, which grow out of the second and third ring of the thorax in the shape of short, folded bags, very similar indeed to the first rudiments of wings in *Neuroptera*. These appendages rapidly enlarge, and when the caterpillar casts its skin, they have already attained a considerable size. But, instead of remaining free, they are soldered to the body of the pupa, the outer wings become hard, and form what have generally been called the wing-covers, resembling then very much the wings of *Coleoptera*. But the jaws have undergone greater changes. They are now transformed into long appendages, similar to the articulated threads which constitute the sucking apparatus of *Hemiptera* and some *Diptera*. The resemblance of the jaws of *Lepidoptera* at this period to those of *Hemiptera* is so great, that we may truly say, that the form of this apparatus in the pupa completely exemplifies the permanent structure of the sucking apparatus in *Hemiptera*; and the hardness of the wing-covers reminds us at the same time of the hardness of the base of the upper wings in the greater part of *Hemiptera*; so that *Hemiptera*, in their perfect condition, would correspond to the earliest condition of the pupæ of *Lepidoptera*. So the higher degree of locomotive power of these parts in *Diptera* would remind us of the condition of the jaws in the *Lepidoptera*, at the moment the perfect butterfly leaves its pupa, when the pieces of the mouth move independently of each other, as is the case with the piercers of most *Diptera*, which remain free, while in *Lepidoptera* they finally form the articulated proboscis. This type of jaws of the *Diptera*, intermediate between those of *Hemiptera* and the perfect *Lepidoptera*, would therefore assign to them also an intermediate position in the system.

Again, the peculiar development of the wings, the anterior of which become perfect and membranous in *Diptera*, while the posterior ones remain rudimentary, shows plainly that in the character of their wings, as well as in all other respects, *Lepidoptera* rank highest among *Haustellata*, and therefore highest among all insects.

Whatever be now the value of these considerations, it must be obvious to all those familiar with the subject, that such a classification differs radically from the classifications founded upon metamorphosis simply. For here the system is founded, not merely upon the fact of the insects undergoing changes to various extent, but upon the nature of the changes themselves. This is a genetic classification, based upon embryological changes, while the classification of the physico-philosophers rests simply upon the circumstance of the insects undergoing metamorphoses or not, without direct reference to the particular character of the successive changes. They bring together *Hemiptera* and *Orthoptera*, because both undergo hardly any changes after they have been hatched from the egg. But here it is shown that the peculiarities which characterize *Hemiptera* correspond, to a certain degree, to the transformations which *Lepidoptera* undergo, and that *Hemiptera* therefore appear, upon embryological data, to belong to the same series, to which we must also refer *Diptera* and *Lepidoptera*, but from which *Orthoptera* are excluded. Again, accord-

ing to the views of the physico-philosophers, the Coleoptera, Neuroptera, Hymenoptera, Diptera, and Lepidoptera belong together, because they undergo extensive changes in their metamorphoses. But I have already shown that, however extensive these metamorphoses may be, they do not rise in any of these orders beyond the development which the Lepidoptera attain in their pupa condition; as in the pupa of Lepidoptera the jaws are already transformed into a sucker-like proboscis, when wings and legs are developed; while Coleoptera, Orthoptera, and Hymenoptera have arrived at their mature condition before the jaws have reached a higher development of structure than that which is exemplified in the metamorphoses of Lepidoptera before they fully pass into the condition of their pupa. So that, notwithstanding their extensive metamorphoses, the mandibulate insects must be placed altogether below the haustellate, even below the Hemiptera; and thus the classification proposed at the outset seems fully justified by embryological evidence; and, if I am not mistaken, we shall in future consider Mandibulata as forming one great natural division among insects, to be placed below the Haustellata.

This conclusion furnishes another illustration of the fallacy of our reasoning, when we allow ourselves to be guided simply by analogy derived from other classes. If among the higher animals we had not a natural series passing from man, through monkeys, to the carnivorous animals, I doubt very much whether we should ever have been led to consider the muscular power and the strength of the jaws as indicating anywhere a higher degree of organization. But this impression, which is correct among Mammalia, can no longer obtain in other classes. We should, on the contrary, be better advised, by this evidence, and in future derive our views, as far as possible, solely from the classes to which they are to be applied.

The same evidence which shows Lepidoptera to rank highest among Insects, shows also that Insects as a class rank higher than Crustacea. And it will not be out of place to remember here the happy suggestion of Oken, who says, that "Lepidoptera are born as Worms, then pass into the condition of Crustacea, and are finally developed into true Insects, exemplifying the natural order of gradation of the three classes of Articulata."

The detailed history of the metamorphoses of some Lepidoptera will sustain more fully the views introduced in the preceding pages.

II. THE METAMORPHOSES OF EUDAMUS TITYRUS.

THERE is no order in the class of Insects the transformations of which have been more extensively studied than those of Lepidoptera. The knowledge of their earlier condition has been of late so much extended, that entomologists have even derived many important characters for their classification from the investigations of these earlier stages of growth. There are, however, several subjects of importance, in a physiological point of view, to which attention has not been sufficiently directed. Though we know the different forms of the larva, of the pupa, and the perfect insect, and though in most cases Lepidoptera may now be recognized in either of these conditions, the manner in which the changes are brought about has not been sufficiently examined.

Caterpillars as such have been minutely described and figured. The differences they show in form and color, and even in the details of their external appendages, have been noticed in most species. The chrysalis, also, has generally been described and figured, though perhaps not with the same degree of minuteness as the caterpillar, whilst nothing can exceed the minuteness and precision with which naturalists have described and figured the perfect insects. Indeed, the illustrative works we now possess of this class exceed in beauty, perfection of execution, and minuteness of detail and coloring, all the illustrations of a similar kind relating to other classes. But those periods of transition in the life of *Lepidoptera*, those short intervals during which the caterpillar passes into the state of a pupa, and the pupa, again, into the condition of the perfect winged butterfly, have been more neglected, probably for the very obvious reason, that, during these periods, as is well known, those animals are more delicate, and more apt to die or to be injured if disturbed.

Perceiving, however, the importance of a close investigation of these stages in their metamorphosis, with reference to a full understanding of the process by which a lively, ornamented worm passes into the condition of a mean, enfeebled, mummy-like animal, inclosed in a hard case, deprived of external appendages of any kind, — and then, again, of the process by which this passes into an insect provided with well-articulated legs, a long proboscis, prominent antennæ, and large wings adorned with diversified colors, — I undertook to secure a sufficient number of larvæ of several species of *Lepidoptera*, to afford me ample opportunities for deliberately investigating them during the period of their transformation. Some of the results of these researches I shall now relate.

In order not to be misunderstood, I would mention that I allude here to the actual transition from one of the temporary stages in the metamorphosis of these insects to another, that is to say, to the passage of the caterpillar to the chrysalis, and that of the chrysalis to the perfect *Lepidopter*, and not to the different stages under which these insects appear temporarily for a longer or shorter time, and which are already so well known. Nor do I mean to introduce the subject of the changes in the internal structure during those metamorphoses, which have been so ably investigated by Herold. My chief object is to illustrate comparatively the morphology of these different stages in their transitions into each other.

As the most prominent and striking changes occur in the external form, my first object was to investigate the structure of the skin, especially of its inner layers, which seem to be the seat of a peculiar activity in this process of transformation. But I must confess that, up to this day, I have been unable to ascertain how the new skin develops under the old, at each moulting, in any of the insects. I can only suggest that the fact of extensive blood-currents flowing over the lower part of the body, and upwards along the lateral walls of each ring, to meet again the dorsal vessel, is very probably connected with this important function, and increased activity of the skin. But how the new layers are deposited, how the appendages themselves, which are successively modified, or entirely formed anew, are developed, and what is the nature of the function by which they are produced, I am unable to state. The results at which I have arrived do not go beyond an illustration of the

comparative morphology of these parts. But perhaps this beginning will successfully lead to a full understanding of the phenomenon; and as these facts were chiefly traced from the larva of *Eudamus Tityrus*, I shall describe more particularly what I have observed in that species, and occasionally introduce some reference to what I have seen in others.

This butterfly lays its eggs separately, one by one, (Fig. 1, egg of natural size,) upon the leaves of *Robinia viscosa* and *pseudacacia*, to which they are attached by a broad, flattened surface. The walls of this attached surface are smooth, and much thinner than the other part of the circumference of the eggs, which is otherwise almost spherical (Fig. 1, *a*). Its color is grass-green. The upper rounded end shows a small circular depression (Fig. 1, *b*), also thinner than the sides. The sides are adorned by sixteen vertical ribs (Fig. 1, *b* and *a**), which are denticulated externally, eight of the ribs meeting the upper circular depression, while eight are shorter. Some time before the caterpillar is hatched, it appears like a dark reddish-brown band across the egg, about the middle of its height. At a later period, and not long before it is hatched, the caterpillar may be seen through the shell of the egg moving in jerks within its cavity. Its darker reddish color renders it then very conspicuous. Though I have often tried to secure a sufficient number of these eggs, I have not been able to trace the mode of formation of the larva itself within the egg, and its changes during its ovarian growth. For those eggs which I have had an opportunity of investigating, and one of which is represented in Fig. 1, I am indebted to Dr. T. W. Harris, of Harvard University, whose extensive knowledge and acquaintance with the metamorphoses of insects are too well known in the scientific world to require notice from me. I can only state, that, when hatched, the young caterpillar has the same form that it preserves throughout its growth.

The head is already dark blackish, and shows two small orange spots above the outside of the mandibles. The collar is also darker than the following joints. However, the color of the main body at that period does not contrast so much with that of the head and collar as it does afterwards; the second and third thoracic joints, and the whole series of abdominal joints being then reddish-orange, and assuming only after the first moulting the same greenish-yellow color which it has afterwards, and which is the final color of the animal. This fundamental color, however, is not uniform, as we observe minute blackish spots about the stigmata, and also upon the back, as well as several small greenish-black streaks across each ring. (Figs. 2, 3, 4, 5, 6.) The thoracic legs are reddish, and the prolegs somewhat orange. As in all caterpillars of *Lepidoptera*, the number of joints of the body is thirteen, the head being considered as one, though, from various indications, we may admit that it consists itself of three soldered segments. The thorax has three joints, provided with three pairs of horny feet, terminating in a claw. There is, however, a marked difference in the caterpillar between these three joints; the first being smaller and shorter than the second, and of a dark reddish-black color, the joint between the head and collar reddish, and the collar itself reddish-

* One of the ribs is still further enlarged in Fig. 1, *c*.

brown, or blackish. Of the following abdominal rings, the first and second, or the fourth and fifth behind the head, are deprived of locomotive appendages, but the third, fourth, fifth, and sixth, or sixth, seventh, eighth, and ninth, are provided each with a pair of ambulatory feet, the extremity of which is surrounded by a crown of minute hooks. The next two joints are deprived of legs, but the last joint is again provided with a pair of prolegs, differing somewhat from the middle ones in being more compressed laterally.

With these characters the caterpillar arrives at its maturity, and when it has done eating, after walking about for some time in search of a convenient place for its transformation into a pupa, fixes itself with some silk threads by the tail, throws a few others across its body, and spins a very thin, transparent, loose cocoon, or rather a kind of incoherent net, between the leaves which it folds around itself, and remains quiet to undergo its first great change, and to pass into the state of chrysalis. (Fig. 7.)

The first marked modification from its former condition consists in a general shortening of the body. (Figs. 8, 9, 10.) The whole larva contracts for about one third of its length, and thus assumes permanently a position which it shows sometimes when at rest. But even after it has thus become quiet, it will, when disturbed, again move about in search of a more protected shelter.

If left undisturbed, the body is seen to swell, especially in its anterior part, which seems to be in a state of chronic inflammation, as it were, having the appearance of an œdematous swelling, distended by a considerable accumulation of lymph.

The thoracic region and the head are at this time the chief seats of the formative process, and of a more active process of nourishment; the other parts seeming rather to wither, the skin to shrivel, and the prolegs to dry up. Indeed, before long, the skin of the larva is sufficiently loose to be separated without much difficulty from the pupa forming underneath; and by watching carefully the moment when the skin splits upon the back in the process of being naturally removed, the whole process may, with some assistance, be accelerated, and the skin turned away before the chrysalis is entirely formed. (Figs. 11, 12, 13.) At this moment the young animal presents characters so different from the perfect pupa, that, unless the whole process has been carefully watched, no one would suppose that the forms it then exhibits are really the next transformation of the larva towards its change into a chrysalis.

Indeed the chrysalis, when perfect (Fig. 7, 7 *a*, 7 *b*), presents a hard case, upon which, with some attention, we may distinguish the outlines of the abdominal joints and the thorax; upon the sides of this, and below it, an outline of the future wings may be recognized, as well as superficial indications of the legs underneath, bent backwards between the wing-covers; there is likewise a tubular flattened case, representing the antennæ; and upon the middle line, a similar one answering to the proboscis. (Fig. 7.) All these parts are soldered together, and upon the skin itself, so closely as to be entirely immovable, and to appear rather as a protecting envelope of the organs, the form of which they foreshadow, than as these

organs themselves. Nevertheless, if we carefully watch the process of the last moulting, or, rather, if we are successful in removing gently the larva-skin before the pupa is hardened, we see that all the above-mentioned organs exist in reality, wholly independent and entirely free from each other, (Figs. 14, 15, 16, 16 *a*, 17, 18, 19, 19 *a*,) though still imperfectly developed, since the legs are mere cylindrical tubes without regular articulations (*a*, *a*); since the antennæ present a similar tubular appearance, somewhat swollen towards the end, but without joints (*b*, *b*); since the maxillæ project as two independent tubes, also very much like another pair of legs (*c*, *c*); and since the wings appear as four distinct, swollen, but somewhat flattened vesicles (*d*, *d*), identical in appearance with the lateral respiratory vesicles of Annelides, sufficiently large, however, to remind us of the wings as they appear when the perfect insect has come out from the chrysalis. We have, therefore, an apparently complete butterfly, somewhat imperfect in its characters, coming out from the larva with all its parts independent, prior to the period when these parts are pressed upon the sides of the animal, and soldered with its walls.

The process by which these parts are pressed flat, and made to adhere to the body, is connected, no doubt, with the act by which the pupa escapes through the narrow slit on the back of the skin of its larva; but when the larva-skin is gently removed, and the pressure prevented, these parts will all remain free, and dry up in an irregular connection, and shrivel in an irregular fusion. Or if, immediately after the removal of the larva-skin, the young animal be placed in water with a few drops of alcohol, the parts will remain expanded, and may afterwards be preserved in that condition in a stronger liquid. So that we may derive imperfect butterflies directly from larvæ, sufficiently similar to the butterfly which escapes from the pupa to be readily recognized, and presenting all the characters of the perfect butterfly, except the imperfect articulations of the legs and antennæ, the unconnected maxillæ, and the vesicular wings.*

The position of these wings is rather symmetrical. They are bent backwards and downwards, the upper surface outside; and this is the case even in those Lepidoptera which, when full grown, fold their wings upwards, with the upper surface turned inwards, and the inner or under surface outwards. This fact is of great importance, as it shows that all the Lepidoptera, which naturally keep their wings bent downwards in the form of a roof, must be considered as lower, in their

* These facts, which I believed to be entirely new to science when I first observed them, have already been noticed to some extent, and are mentioned in the following manner by Burmeister, in his Manual of Entomology, p. 426 of the English translation:—"After the third moulting, when the larva has acquired its full size, the rudiments of the wings begin to form beneath the skin, upon the first and second segments. They at first present themselves as short viscous leaves, the substance of which greatly resembles that of the mucous tunic, and to which many delicate trachææ pass, which distribute themselves throughout them. These rudiments increase with the growth of the caterpillar, and betray themselves, even externally, by both the segments of the caterpillar, upon which these rudimentary wings are found, appearing swollen and spotted. Their enlargement probably takes place by the assistance of the blood flowing into them. Simultaneously with the perfecting of these rudiments, the intestinal canal increases in compass, and, as a consequence of this increase, there is a greater accumulation of the fatty mass. A

respective families, than those which raise them upwards. We may, therefore, learn from this fact, that the diurnal *Lepidoptera* rank higher than the crepuscular and nocturnal ones. This hint would, of itself, be an ample reward for the time spent in these investigations, even if we did not further learn from them that there is a strict homology between the wings of butterflies and the respiratory vesicles of *Annellides*, and that the physico-philosophers (I mean particularly the acute Oken) are fully sustained by material facts when they assert that insect-wings are transformed gills.

When the metamorphosis of the larva is allowed to go on undisturbed, this immature butterfly, with a comparatively long abdomen, still further contracts. The abdomen especially is considerably shortened (Figs. 17, 18, 19, 19 *a*) and thickened, though its joints remain movable. But the head and thorax and all their appendages are soldered together, and form a solid, immovable case; and the connection of the external appendages becomes so intimate, that, instead of appearing like independent parts, they assume rather the appearance of outlines of those organs carved upon a surface, as if they were mere indications of the parts to be developed in these regions (Figs. 20, 21, 22), but seeming to be as yet unformed. Nevertheless, as I have shown above, they were all independent shortly before, and have become gradually more and more united in the perfect pupa.

This transformation is, again, of very great importance with reference to our classification of articulated animals, as it shows that the condition of those *Articulata* in which head and thorax are united is a lower degree of development than the condition of those in which head and thorax are distinct. We have, indeed, here an additional evidence of the views which I have maintained on another occasion, that the *Crustacea* — in which the thoracic and cephalic joints are either entirely independent of each other, as in the larvæ of *Lepidoptera*, or united in one continuous case, the cephalo-thorax — rank below the true *Insects*, and also that *Arachnidæ*, the spiders, are inferior to the *Insects* proper.

The transformation of the pupa into the perfect insect (Fig. 23) takes place in the same manner as the transformation of the larva into a pupa, in consequence of another moulting, during which the surface of the animal undergoes its last changes, and assumes the characteristic peculiarities of the perfect insect. The difference, however, between the perfect *Lepidopteron* and the pupa is much less than the

transformation is also taking place in the anterior feet of the caterpillar, for the larger legs of the butterfly begin to form. But, as a similar transformation is going on in the oral organs, the caterpillar loses its desire to eat and power of mastication, it ceases to receive food, and prepares itself for its last moulting, namely, for its change into the pupa. It seeks for this purpose an appropriate place, where it can lie, hang, spin, or attach itself, and it accomplishes this, its last business, the same as its earlier ones, with great care and consideration. After its situation and web are prepared, it reposes a few days, then strips off its skin, and now presents itself as a pupa, with the visible limits of a butterfly."

It is surprising that this observation should not have led its able author to trace these facts further, and to recognize their bearing upon the classification of *Articulata* in general, and that of *Insects* in particular, as well as upon the appreciation of the relative value of the organs in the various development they present in this type of animals.

difference between the pupa and caterpillar, though the contrary would seem to be the case. However, from what I have said above, it is plain that the Lepidopteron arises from the larva with most of its perfect features, only developed in a less finished manner, while the changes which the animal undergoes during the pupa state only consist, as it were, in the last perfecting of the final development already introduced during the last period of the larval life.

The skin of the pupa, having acquired its complete hardness, the appendages having been soldered together, and now constituting a continuous case, in which skin, legs, wings, antennæ, and jaws are fused together, is gradually separated from another more perfect envelope, which is to be the last covering of the last period of life of the butterfly. All the ornamented appendages of this skin, — its well-articulated legs, its feathery wings, its articulated antennæ, its faceted eyes, its elongated movable maxillæ, — when perfect, remain separate from each other, movable upon each other, and independent in their functions, and do not undergo again a fusion similar to that by which the case of the pupa was formed and thickened. The only connection which grows more intimate in the perfect animal than it was in the pupa is that of the two maxillæ, which henceforth are united along the middle line, and between which a groove is left to form the curved proboscis. Gradually all these parts are loosened from the inner surface of the pupa-case, they acquire their peculiar coloring, and, the pupa-case bursting upon the back, the perfect insect comes out in all its beauty. At first the wings, however, are shorter and narrower than afterwards, when they have been expanded, stretched, and moved to prepare for their final function. Sometimes, before being hatched, the process of these last changes may be noticed through the skin of the pupa, which grows more transparent in proportion as it is loosened from the surface of the insect within. A row of variously colored dots in *Danais Archippus*, for instance, points out the position of the wings, as well as their extent. In this butterfly the pupa-case is particularly transparent. The colors show most distinctly through the envelope thirty-six to forty-eight hours before the perfect insect comes out, and, in general, a change of color of the pupa is an indication of its advancing maturity. In some degree the perfect wings are folded, but they actually grow, as well as expand, soon after the butterfly has left its pupal envelope, and begins to lead that particular life for which it has undergone these changes. It is now ready to pair, and, after fecundation, to lay its eggs, by which the species is preserved, reproduced, and perpetuated.

III. SPECIAL CLASSIFICATION OF LEPIDOPTERA.

In the preceding pages we have described minutely the transformations of *Eudamus Tityrus* within the egg, up to its perfect development as an active butterfly. We have shown that many points in the development of this animal have been entirely overlooked, and that, in general, one stage of the metamorphoses of Lepidoptera has remained, if not entirely unknown to entomologists, at least unappreciated in its bearings. The study of these metamorphoses in the new light in

which it is now presented to us has led to an extensive comparison between these changes of the butterfly, and the permanent states and features of the different families of Insects; and, from this comparison, the necessity of extensive changes in the classification of Insects has been shown, and an entirely revised system, resting upon these new views, has been proposed.

There are now further consequences, following easily from the facts already mentioned, which remain to be traced to their full extent. We have shown the influence the knowledge of these metamorphoses must eventually have upon the classification of Insects at large. We have now further to investigate the bearings of these facts upon the special arrangement of Lepidoptera among themselves, and also to trace out the analogies between those changes of the Lepidoptera and the permanent characters of the other classes of Articulata. For it is not enough to have shown that the classification of Insects has to be modified upon this evidence; we must investigate with equal thoroughness the importance of these facts with reference to the relative position of the different classes which have been distinguished among Articulata in general, and also trace the immediate consequences of a more complete knowledge of the transformations of Lepidoptera, as bearing upon their special arrangement.

Let us first examine the relations of these facts to the special classification of Lepidoptera among themselves. This family, or order, of Insects is generally divided into three natural groups, Diurnal, Crepuscular, and Nocturnal; or Butterflies, Hawk-moths, and Moths; which divisions are by some reduced to two, Diurnal and Nocturnal Lepidoptera, — the Sphinges being then considered simply as a family among Moths, and not as a primary division in the whole order. The question now arises, in what succession these families should be placed, whether we consider the larger groups or the minor subdivisions. Of course, I do not feel prepared to express a decided opinion upon every doubtful point in the classification of Lepidoptera, but simply inquire into the principle of their classification, and try to obtain some light respecting their gradation, from the facts observed in Eudamus. It is generally considered that diurnal Lepidoptera rank highest, and Sphinges are invariably placed between Butterflies and Moths. I have, however, looked in vain, in all the works upon Lepidoptera with which I am acquainted, for arguments intended to justify and sustain this arrangement; and though this order of succession is universally admitted, I do not find that it is anywhere expressly sustained, or that allusion is anywhere made to the evidence that they ought to be considered in that succession, and that this arrangement is intended to express the true relative position of these families. It seems as if this arrangement had been introduced simply for the sake of convenience, by common consent, without having resulted from an inquiry into the subject; or perhaps it has been adopted in consequence of the more extensive knowledge early observers have had of the diurnal Lepidoptera, and from the great difficulty in obtaining and studying the minor species among the nocturnal ones. But whatever may be the cause of this arrangement, so much is plain, that, as soon as the question is raised about its value, it will be found to be still unsettled. I do not, however, oppose the present arrangement. On the

contrary, I am about to show that it is natural, that it agrees with inductions derived from embryological studies, and that it is sustained by facts from various quarters, though some of these facts have remained unnoticed and others have been used unconsciously, or, at all events, never with a view to establish the proper rank of Lepidoptera among themselves.

There is one point in the early metamorphoses of Lepidoptera which is of great importance in this respect; I mean the condition of the larva of diurnal Lepidoptera. Among this family, there is not one species known with maggot-like caterpillars; they are all provided with various kinds of organs of locomotion, legs and prolegs, the last pair of which, again, generally differs from the middle prolegs. They are all colored, and their color is bright and varied. Now this state of development, in which the diurnal Lepidoptera escape from the egg, is already a higher condition than that from which other families among Lepidoptera begin, or of which there are, at least, some examples in various other families. For, even among Sphinges, we have naked larvæ, living in the dark, with an obscure, almost colorless skin. And among nocturnal Lepidoptera the number of those types in which the larvæ are more or less maggot-like is still greater, while among diurnal Lepidoptera all begin with a character of most perfect caterpillars. Again, it is among the nocturnal Lepidoptera that we find the greater number of larvæ resembling Worms proper, or having characters most strongly analogous to those of true Worms.

If, from this state of growth, and the arguments it affords in favor of our view, we pass to the investigation of the pupa, we find here, again, arguments which go to show that the pupæ of the diurnal Lepidoptera have higher characters than those of Sphinges and Moths, as I shall presently show. The caterpillars of Lepidoptera, however highly organized, correspond to that stage of development of Insects in general which we call their larval state, and this homology may be traced through the whole class, however diversified the larvæ of various orders may be. This larval condition corresponds to the state of structure characteristic of the class of Worms. The larvæ of Insects are, indeed, truly homologous to the class of Worms in structure, while their pupæ correspond in the same manner to the class of Crustacea, as I shall show more fully hereafter. If this be the case, let us now compare the pupæ of the different families of Lepidoptera.

Among the nocturnal species, even including the Sphinges, we have those in which the body is smooth, more or less cylindrical, elongated, the abdomen more free and conspicuous, the thorax and head shorter; while the pupæ of all Papilionidæ are angular, the head prominent, the head-chest proportionally longer than the abdomen, with all sorts of protuberances, projecting angles, and spines, and the abdomen comparatively reduced, — characters which seem to me to indicate a remote analogy between the peculiarities characteristic of the long-tailed and short-tailed Crustacea, the relative position of which has long been determined. If, therefore, the general analogy between pupæ and Crustacea be once granted, the more special relation of the diurnal pupæ and Crabs, and that of Moths and Lobsters, must also be granted, and the superiority of the pupæ of diurnal Lepidoptera over the

nocturnal would be also once and for ever established. This seems very natural, as soon as it has been shown that the caterpillar of the diurnal *Lepidoptera* already ranks higher, on the whole, than that of the nocturnal ones. And this being the case, we are naturally led to expect that the next stage in the metamorphosis should bring the next stage of development higher also.

These views might seem, at first, sustained by very slight evidence. But let us now further consider the perfect state of development of these different *Lepidoptera*, and we shall find, not only additional evidence of the view I have taken of this subject, but perhaps still stronger reasons for adopting it. Here, again, I wish to call attention anew and more emphatically to another point in the development of *Eudamus*, and the diurnal *Lepidoptera* in general.

The position of the wing of the perfect butterfly differs widely in its matured condition from its position in the pupa, and to this point entomologists have paid far too little attention, if they have at all noticed the fact. In all *Sphinges* and *Moths* the upper surface of the wings is always turned sideways and upwards, the wing being rolled downwards upon the sides of the larval body; when hatched from the pupa-skin the wings are spread horizontally, or more or less sloping downwards, in the same relation to the body which they had within the pupa, the lower surface of the wings resting upon the body, the upper being turned outwards. There are various modifications in the disposition of these parts: the wings in some sloping more sideways, and still encircling the body as in the pupa; in others being spread flat and horizontally to a greater or less extent, the upper wing, however, overlapping the lower wings very extensively, and almost always covering them wholly in the state of rest, as is the case within the pupa-skin.

Such, however, is not the position of the wings in diurnal *Lepidoptera*. In the mature stage of growth they are raised above the body, the upper surface being turned upwards and inwards, and never turning outwards or sloping downwards; the upper wings spreading in a manner which leaves the under wings uncovered, and neither pair of wings bending downwards, to encircle more or less the body, as is seen among so many of the moths.

But this disposition of the wings, this character of the perfect butterfly, this mode of carrying their organs of locomotion when at rest, or in activity, is peculiar to the *Papilionidæ* only in their perfect state. In their pupa condition the wings are placed precisely as in all other *Lepidoptera*. They are bent downwards, the upper wings covering the lower ones, and the upper surface of the latter being turned sideways. And as no one can doubt that this change in the position and characters of the wings in the diurnal *Lepidoptera* is something which grows out of a condition common to all, it is as plain as any other embryological evidence can be, that the development of diurnal *Lepidoptera* goes beyond what is observed in *Sphinges* and *Phalænæ*. Assigning, therefore, to diurnal *Lepidoptera*, upon mature comparison, a decidedly superior position in their order, the *Skippers*, *Hesperidæ*, would rank next, from the circumstance that they raise the anterior wings only, and stretch the lower ones more or less horizontally.

My special knowledge of *Lepidoptera* is not at present sufficient to carry this

VOL. II. ART. 6. — 3

view through all the minor divisions of the whole order. I trust, however, that I have here introduced a sound principle, by means of which the closer relations of the secondary groups of Lepidoptera may be determined. This much can already be said, — that the degree of inclination of the wings backwards and downwards, and their greater or less extension sideways, indicate the gradation in which the various types of this order should follow each other. For, when unfolding, the wings of diurnal Lepidoptera, which are at first turned backwards, are next stretched sideways before they are raised. In accordance with this fact, the Sphinges, which stretch their wings sideways, and in which the upper wings do not fully cover the lower wings, should rank next to the Papilionidæ, and be followed by Bombyces, Noctuæ, and Geometræ; and the small Pyralidæ, Tortrices, and Tineæ, in which the wings are constantly stretched backwards close to the body, which they encircle more or less, should really rank lowest, as they are generally placed in our entomological works.

What I have said of the wings may be applied to the legs and trophi. From careful examination of the caterpillar and pupa, especially during its transformation from the caterpillar state into the pupa state, and from this into that of the perfect insect, the relative perfection of these organs will be as easily ascertained as that of the wings.

I may add, that the antennæ should be examined in their earlier stages with equal attention; for they are much more uniform in the pupa state, among all families of Insects, than in their perfect condition. I have already been very much struck with the fact, that the antennæ in the pupa of diurnal Lepidoptera are not yet clavate, as they are in the perfect insect, but resemble rather the antennæ of Sphinges, and, in some instances, those of Phalænæ. But my want of knowledge of the special characteristics of Lepidoptera forbids me to enter, at present, into a more extensive and comprehensive comparison.

IV. REMARKS UPON THE METAMORPHOSES OF SOME DIPTEROUS INSECTS.

It is well known that the maggots, which are hatched from the eggs of the meat-fly, and other allied species, undergo no moulting, — that is to say, do not cast their skin during their growth, as the larvæ of most insects do, but preserve, throughout their larval condition, the same exterior envelope, which, in the full-grown larva, is at last contracted, hardened, and transformed into a case similar to the envelope of the common pupa.

This analogy has seemed sufficiently strong to induce entomologists to give the name of *pupa* to that condition of the growing fly; and simply to distinguish it from an ordinary pupa under the name of *pupa coarctata*. These pupæ are sometimes called *cased pupæ*, because they are cased within the skin of the larva. It is further known, that after a certain time perfect flies issue from such pupæ. It would seem, therefore, that the metamorphoses of the Diptera differ considerably from the metamorphoses of other Insects, and that the perfect insect is directly developed under the skin of the larva, without the transition of the worm into a true pupa.

The fact, however, that flies, when hatched from their hard envelope, are often observed to carry after them a thin membranous film, has induced me to inquire more minutely into this case. Having secured a large number of so-called pupæ of the meat-fly, *Musca vomitoria*, I tried to separate their outer coat as soon as it began to harden, and it was probable that the process of further separation of the future perfect insect from its primitive envelope had commenced. I succeeded without much difficulty in tearing off the hard case without damaging in the least the soft animal within, when I found that there was really a true chrysalis* formed under the larva-skin, differing only from ordinary pupæ in the softness of its envelope, which is a simple, transparent, white membrane, presenting in a rudimentary condition all the peculiarities and characteristics which distinguish the perfect fly, but in an imperfect state of development, and very similar to the condition of the young butterfly when it is ready to cast for the last time its larva-skin before it passes into the state of a real pupa.

This transparent chrysalis of the fly shows, like the young pupa of the butterfly, all the parts of the head; rudiments of wings, in the form of short vesicles; three pairs of legs, tubular, unarticulate, bent under the thorax; and distinct joints of the body, already contracted and combined in such a manner as to define in their general outline the head, chest, and abdomen. But that this is a real chrysalis within the larva-skin, and that the difference between the Diptera and the other insects which undergo complete metamorphoses consists simply in the circumstance that the skin of the larva is retained to protect the soft pupa, may be positively concluded from the fact that, within this transparent pupa, we may see, as soon as it is completely separated from the larva-skin, the next stage of development more or less advanced, and the perfect insect appearing within that thin covering. The transparency of the pupa-skin very much facilitates the investigation; as it is easy to see through it all the parts of the perfect insect fully developed at a very early period of the hardening of the larval skin. A week had scarcely passed after my larvæ had ceased to be movable, when, on removing the outer larval covering, I could not only distinguish the perfect pupa, as I have described it above, but within it the well defined parts of the perfect insect, with all their minute characters, could also be satisfactorily distinguished. The legs, which in the pupa were simple, tubular, and unarticulated, were now seen within, with all their joints, hairs, and hooks. The vesicles first representing wings now contained perfect wings, with their nervules and hairs. The eyes with all their facets were well defined. The antennæ also, and all the parts of the mouth, had lost their larval appearance, and assumed the character which they exhibit in the perfect insect. The surface of the rings of the body presented, throughout, the hairy covering and the scales which characterize them, though all these parts were still white, transparent, and entirely soft.

As a striking analogy between the pupa of the fly and that of the mosquito, I may add, that the pupa presented on the sides of the interior part of the thorax

* See also Dr. Harris's Report on the Insects of Massachusetts injurious to Vegetation, pp. 14 and 403.

two little horn-like processes, communicating with the thoracic tracheæ, which are, no doubt, analogous to the two respiratory thoracic tubes of the larva of *Culex*.

These facts seem to me important, not only as showing a greater analogy in the metamorphoses of different insects than has been supposed to exist, but also as affording greater facilities for the study of the transformation of the pupa into the perfect insect than is afforded in other families, where the pupa itself is hard, and prevents the investigator from tracing the final changes which the insect undergoes within its mummy-like envelope while assuming its last forms. But upon this point I am not, at present, prepared to offer further remarks, and would only call the attention of entomologists to the facilities thus afforded for investigation.

V. RELATIVE POSITION OF THE CLASSES OF ARTICULATA.

It is a very strange circumstance, that, in the classification of articulated animals, so little attention has been paid to the metamorphoses as a guide to lead us in our investigations, that comparative anatomy alone has been appealed to for a decision in this question, and that the facts brought forward upon anatomical evidence should have led to an arrangement differing so much from that to which embryology would lead.

It will be remembered that all anatomical zoölogists and all comparative anatomists without exception have considered the Crustacea as highest among Articulata, on the ground of higher structure; being probably influenced by the presence of a heart and the extensive circulation which exists in Crustacea as compared with Insects in which the dorsal vessel faintly reminds us of a heart, and the circulation is so peculiar as to have escaped notice until lately. This inference from anatomical data has, probably, been made under the influence of an old view, from which it is so difficult to divest ourselves, that animals should form a natural series, and may be arranged in one progressive line according to the gradation of their structure. The all-important distinction, introduced by Cuvier, of different types, of four distinct plans of structure, has not yet sufficiently penetrated the spirit of those who have followed in his steps. These four types are not universally acknowledged as independent; they are not constantly viewed as centres radiating in different directions, as they ought to be. Their relative connection with each other is more generally considered than their peculiarities as distinct types. For, if these great divisions of the animal kingdom were fully understood as distinct types, it would follow naturally in the mind of every one, that what might be a character of superiority in one group might not be so in the other; what might lead to natural combinations in one department might mislead in the estimation of relations in another; and the final impression would be, that in each type there is a peculiar ruling principle, which must be considered by itself; and that we are not allowed to bring the four types into connection with each other, unless upon the most general considerations, when investigating the foundation of animal life in its different general tendencies, and comparing these tendencies with each other to find out their common foundation as well as their difference. But as soon as we enter into any

details, as soon as from these generalizations we begin to investigate the peculiarities of each type, then let us be guided by special principles, and no longer by the general abstract laws of life.

Now, in the type of *Articulata*, we have division of the body, articulation of the limbs, development of joints, external evolution of parts, and multiplication and independence of these parts, prominent in every type under most diversified modifications; and these peculiarities characterize the type of *Articulata*. External metamorphosis is, perhaps, on the whole, the most prominent feature of this type; that is, extensive changes in the external appearances of the body, — changes which follow in regular succession at definite periods of life, and introduce successively such modifications in some of these animals, in which the metamorphosis is most extensive, as completely to alter their appearance; so much so, that only direct observation of successive generations can satisfy us that, under these different forms, we have really the different stages of growth of one and the same animal. The study of these changes of form is the more important, as the structure changes at the same time; for here changes of the form and of the structure are so closely related as to be simultaneous.

Now it is a principle which must be acknowledged universally, that in the growth of animals their successive changes are progressive, — are steps forwards, — an advance from a lower to a higher condition. However evident the decrepitude of old age may be in the structure of an animal, as long, at least, as it grows and successively assumes new changes, we cannot for a moment suspect that these changes are retrograde steps in the organization. This must be granted even in the presence of the deformed appearance and extreme growth of pregnant individuals, or of females preparing for reproduction, among parasitic *Crustacea*. For here we observe a kind of metamorphosis which has no longer a direct bearing upon the growth of the individual, but has reference to its reproduction. I insist upon this point, as otherwise the principle of progressive development might be questioned even in its fundamental consequences.

But as soon as it is granted that the young animal is less perfect than the mature one, as can be shown by tracing its development from the egg, it will follow as a matter of course that the metamorphoses of *Articulata*, considered in general, must be the safest guide to a just appreciation of the relative position of the secondary groups in the whole type. The most perfect metamorphoses are known among *Insects*. They appear in their caterpillar, pupa, and perfect state. But these metamorphoses have various degrees in different families. The larvæ of all *Insects* are not equally advanced when they are hatched from the egg. In some, the larva comes out as a naked, colorless worm, without any appendages; in others, it has simple legs of one kind; in others, there are various sorts of legs, and the body is variously colored and provided with external appendages; in others, the larval development takes place altogether within the egg, and the young insect is hatched in the form of the parent, wanting only wings. But in all these different conditions the larva is, undoubtedly, inferior to the pupa. The pupa state of *Insects* is the period of their development which, at the present time, stands most in need of further investiga-

tions and extensive comparisons; for it is not now very well understood, nor is its character fully and justly appreciated.

From its appearance among Lepidoptera, it is generally represented as a dormant state in the development of the young butterfly, as a sort of mummy almost without life; while, in reality, it is a period of the most extensive organic activity, during which the greatest changes are going on in the structure preparatory to the appearance of the perfect insect. When the butterfly leaves the pupa, it undergoes no further organic change; all the changes took place chiefly during the period when the caterpillar was transformed into a pupa, and during the pupa state itself. This stage of growth is therefore to be considered as one of the most important periods in the development of the insect, just as the growth within the egg is with reference to the caterpillar. The homogeneous cellular mass which constitutes the egg gives rise to the caterpillar; when hatched, it is already fully developed as a caterpillar, and grows only to a larger size as such; but its structure, as far as it is characteristic of that state, is introduced during the metamorphosis of the substance of the egg from which it arises, in the same manner as the perfect insect is formed from the changes which the caterpillar undergoes under its last skin, and during the earlier part of its pupa state. These are the two great periods of development; the other periods are periods of growth. The caterpillar feeds upon large quantities of food, grows to a larger size, and stores up large quantities of organic matter, out of which, by another extensive metamorphosis, the perfect insect is developed; which, when mature, lives only to reproduce its kind. Up to that period the development is decidedly progressive, and up to that period we see even those articulated animals which undergo a so-called retrograde development advance in their metamorphosis from lower to higher structures, from a simpler to a more complex organization.

Now, are not the insects which undergo the most extensive metamorphoses to be considered as the standards from which the forms of other articulated animals have to be appreciated? Is not the fact, that caterpillars bear so close a resemblance to Worms, a sufficient indication that the Worms rank lower than Insects? No serious objection can be made to this principle; and if so, may not the relative position of Crustacea between Worms and Insects be determined upon the same principle? It can be shown that we have no other safe guide to determine the true relation between the different classes of articulated animals.

Let us first compare, more fully, the larval condition of Insects with adult Worms. And here I cannot but regret that the larvæ of Insects have not all been so carefully studied as those of Lepidoptera, and more minutely described and figured than they are in our entomological works; for, generally, all that is given there has mere reference to their general form, and even the external parts are not always described and figured with sufficient accuracy. It seems as if a knowledge of the external forms only were to be acquired; and as if the morphology and structure of the parts in their successive changes were of no consequence to the appreciation of the affinity of animals before they have attained their final development. However, we find among Insects larvæ entirely destitute of external appendages, the body consisting of several uniform joints, and the head being scarcely distinct from the other articu-

lations. In the aquatic species of that kind, there are external, gill-like, respiratory organs, while in the terrestrial ones the respiration takes place through stigmata and tracheæ. In others the head is more developed, the joints of the body less uniform, appendages to some joints are developed, and the whole larva assumes more fully the appearance of a terrestrial animal. In a higher condition still, we see these larvæ brightly colored, the head well distinguished, peculiar feet attached to the anterior rings of the body, and feet of another kind to several posterior joints; larvæ of this description begin to resemble the perfect insects which are developed from them, in almost every respect save that they are destitute of wings. In numbers of them there are, in addition to the legs, appendages developed upon all the rings of which the body consists, which give them a most remarkable appearance. Now, if we take into view all these different forms of larvæ throughout the class of Insects, without reference to the peculiar types of winged insects which arise from them, and institute a comparison between them and Worms, we cannot fail to be struck with the remarkable analogy which exists between them. The naked larvæ correspond to the naked Worms, and the larvæ provided with appendages resemble the Dorsibranchiate and Tubulibranchiate Worms in so close a manner, that particular genera of Worms might be singled out as corresponding most closely to different forms of larvæ among Insects. The larvæ of Limacodes, for instance, can be considered as terrestrial representatives of the genus *Polynoë*; the larvæ of Bombyces correspond to the Nereid Worms, while some among the larvæ of *Papilio* proper, with their protractile branching appendages upon the neck, remind us of *Terebella*. It would seem as if the larvæ of Lepidoptera began their life in a condition analogous to that of the higher Worms, and as if they had no analogy to the lowest types of Worms, that is, to the Helminths or Intestinal Worms. However, this were a very incomplete view of the subject, for these larvæ within the egg show a still lower organization, and forms and structures which are as closely analogous to the forms and to the structures of Intestinal Worms as those of full-grown larvæ are to the higher Worms.

Now the special characters of Worms as a class consist precisely in the peculiarities which distinguish the caterpillar from the perfect insect. Their body consists of numerous uniform joints, the head being scarcely distinguished from the body, or, at least, the head only being distinguished, — the appendages to the joints being diversified equally upon all the joints, or entirely wanting, and wings never being developed upon them in any of their stages of growth. Further analogies might be traced, there being Worms with external gills, as we notice among certain larvæ of insects; others, the Earthworm for instance, with aerial respiratory organs, as are most larvæ of Insects. Some are entirely blind, others provided with many ocelli. The internal structure also might be compared, with the same results; but it will suffice to hint at it, to recall at once to the minds of zoölogists and anatomists the difference which exists between the internal structure of larvæ and that of the perfect insect, and the resemblance the larvæ show, on the contrary, to the structure of Worms.

The question respecting the position of Crustacea among articulated animals is

one of greater difficulty. There is something imposing in the larger size, in the greater strength, in the powerful appendages, in the perfect circulation, of crabs and lobsters, and I do not wonder that, from these inducements, so many naturalists have been led to the idea that Crustacea rank highest among Articulata. But there are also among these animals so many of an inferior size, almost microscopic, and with so simple structure, especially among the parasites, that there is no reason for being too strongly impressed by the superior size of the smaller number. But let us examine what is the value of these characters, and how we should compare the Crustacea to other articulated animals to arrive at rational conclusions.

As a class, Crustacea are characterized by an arrangement of their joints which is peculiar to them. The single rings of which their body consists are no longer uniform. They may be similar, they may be free, but there is always considerable difference between them, and they are always provided with locomotive appendages of some kind or other. There is scarcely a type among them so low as most Worms; and I venture to say that there is no one among them which ranks as high as Insects. For in Crustacea, whatever be the diversity in the joints, they are all more or less provided with locomotive appendages; these animals all breathe with gills, and the development of the circulatory apparatus is, in all, in accordance with this particular mode of breathing, as it is a general fact, that gill-breathing animals have a well supplied circulation of blood. We need only consider the Fishes, and even the Gasteropoda and Cephalopoda, or compare the Worms provided with gills with those which breathe in a different way, to be satisfied of the fact. So that, in my opinion, the development of the circulation in Crustacea is no absolute indication of their higher rank, and we shall be still less disposed to assign to them so high a position, as soon as we examine them in a morphological point of view.

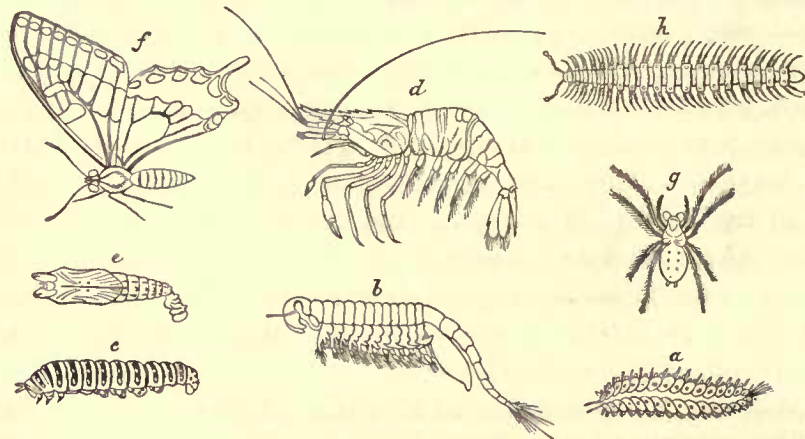
It is well known that their body consists of a number of joints, which is frequently larger than the number of joints in Insects, and even larger than that of the larvæ of Insects, coming, in this respect, nearer to the Worms than to the Insects, in whatever state we may compare them together. A larger number of joints among articulated animals is so constant a character of inferiority, that we must not overlook this important fact, when inquiring into the natural position of Crustacea. Again, these joints are more extensively free than they are among Insects, — nearly as much so as among Worms, — or they are soldered into a solid box, as in Crabs; while there is no perfect true Insect in which the joints are not combined into three distinct regions, head, chest, and abdomen. Moreover, the joints in Crustacea are all provided with locomotive appendages; in Insects they are so only in the larval condition, and the locomotive appendages are reduced in number, and confined to the chest, in their perfect state; for even the claw of a lobster resembles more the paddle of its tail, than the true legs of an insect larva resemble its prolegs. The jaws of Insects undergo such changes, that they assume forms and functions differing far more from those of the legs than among Crustacea, in which various pairs of the masticatory apparatus have still the common form of legs. Their other appendages, such as the eyes and antennæ, are also in Insects more remote from the common type of such appendages than they are among Crustacea. So that

there is a distinct inferiority of development in all these respects among Crustacea when contrasted with true Insects, which should leave scarcely a doubt in our minds that this class as a whole is inferior to the class of Insects as a whole.

But there is another point in this question which, in my opinion, settles definitely the relative position of Crustacea between Worms and Insects. Wherever the joints of their body unite to form distinct regions, they combine in such a manner as to form only two well-defined divisions: the tail, or rather abdomen, with free, movable joints, and the rings of the head and chest, united into one continuous shield above, though below they may present more or less distinct indications of their primitive separation. Head and chest united, and abdomen free and movable, with morphologically homogeneous appendages upon all the joints, — such is the character of the highest Crustacea. Now, in the development of true Insects we have a stage of growth when these animals assume precisely the same condition. It is that of the pupa. Before the insect assumes its final winged state, the rings of the anterior part of the body are soldered together more closely, and the abdomen alone remains free and movable. The lower wings, with a somewhat gill-like structure, which, for a time, are free in the young pupa, are soldered upon the inner surface of the upper wings, which themselves adhere to the chest. The jaws and legs are almost identical, and it may be said that a pupa corresponds, in its main features, to that combination of characters among Articulata which is peculiar to the Crustacea. Indeed, what is the pupa among Insects? It is that state in their development in which the anterior joints, which were free in the larva, are fused into one distinct region, no longer endowed with free movements; but in which the joints of the abdomen still remain movable. This answers most remarkably to the structure, form, and adaptations of the body of Crustacea. And this being the case, I consider the position of the whole class as settled. It is intermediate between Worms and Insects; for, in the general development of Insects, the pupa state, which corresponds to the Crustacea, is the intermediate state between the worm-like larva and the perfect insect. Worms, therefore, are the lowest class among Articulata, the Crustacea the next class above, and Insects the highest class of that type. Of course, in this arrangement we give up all possibility of bringing the higher type of Articulata in any way near the lower types of any of the other great divisions of the animal kingdom, with which it might seem natural to combine them in one continuous series; as, for instance, with the lowest of the Vertebrata. But such attempts are precisely what I have objected to in our classifications; while, upon the arrangement I propose, the type of Articulata in all its peculiarities is gradually wrought out more and more fully, and in its highest class recedes most from all other types. The impossibility of combining the type of Articulata, by its highest families, with any of the other types, I consider as one of the most valuable features in my classification. I know very well that some of the Annelides have been mentioned as constituting a link between Articulata and Vertebrata through the Myxinoids. But who would, in the present state of our knowledge, place Annelides above Insects and Crustacea, because they have colored blood, when their relation to Helminths is so plainly ascertained? It seems to me far more rational to trace the

analogy which exists between the lowest families of all the four great types of the animal kingdom, and to consider these different types as rising from a common base, in four different directions, to different heights of development, at which they differ most widely. The analogy between the lowest Worms, with their embryonic characters, the lowest Polyp-like Mollusca, and the lowest Radiata, is a far more prominent feature in the animal kingdom than the collateral analogies which exist between their higher families.

There is another feature in the affinities of the articulated animals, which, in this classification, is more fully brought out, and which otherwise can hardly be traced, — the fact that the lower Crustacea resemble Worms nearly as much as the young Insects; and that here, again, we have in the three classes of this type a repetition of the leading feature which we have noticed when comparing the four great types together, — the Worms beginning with a worm-like form, which they preserve through life, — the Crustacea beginning with a worm-like form, or with worm-like inferior types, rising in their highest families to the type of pupæ, — and the Insects beginning with a worm-like form, transforming into pupæ, or, in other words, assuming temporarily the type of Crustacea, and attaining finally to their highest state, that of winged Insects.



The wood-cut here annexed will give a graphic picture of this correspondence. Fig. *a* represents *Polynoë squamata*, as a type of the class of Worms. Fig. *b* represents *Branchipus stagnalis*, as a type of the lower Crustacea, exemplifying at the same time their analogy to the Worms and to the larval condition of the higher Crustacea, of which Fig. *d* represents a characteristic species, the common shrimp of Europe, *Palemon serratus*. Fig. *c* represents the caterpillar of *Papilio Asterias*, which has a close resemblance to some of the higher Worms of the family of *Tubicolæ*. Fig. *e* represents the pupa of the same Butterfly; its analogy to the higher Crustacea, which consists in the combination of the rings into two distinct regions, cannot be overlooked. Finally, Fig. *f* represents a perfect Butterfly, in a state of development which is not attained by any type of the great division of *Articulata* except Insects.

At this stage of the investigation, I venture to say that I have myself already traced, to some extent, the analogy which exists between the various forms of

pupæ and the different types of Crustacea, and that I have satisfied myself that it will successively be found more and more intimate, and give finally to this classification the character of a true genetic natural arrangement.

With reference to the class of Insects, there are some particular points which require especial study. It is well known that among air-breathing Articulata there have been several classes distinguished under the name of Insects proper, Arachnidians, and Myriapoda, and there are several groups intermediate between the two latter, which stand almost isolated, and were formerly united under the common name of Apteræ. The question now arises, how these are to be regarded with reference to the true Insects, and whether they should form intermediate classes between Crustacea and Insects, or be united with the Insects proper as one class.

As far as the Arachnidians are concerned, I entertain no doubt that they cannot be considered as a class by themselves, but must be decidedly united with the Insects; for the peculiarities in their structure upon which the separation rests hardly justify such a primordial distinction. The difference, as it has been given, is chiefly derived from the number of legs, and from the respiratory apparatus; there being in the true Insects only three pairs of legs, while in Spiders there are four, and the respiratory organs of Insects being true trachææ, and those of spiders lung-like sacs. But this greater number of locomotive appendages indicates only a lower degree of structure, rather than a classic difference. Again, the difference in the structure of the respiratory organs is rather morphological than essential, as Dr. R. Leuckardt has recently shown. So that the chief ground for a distinction of the Spiders as a class is illusory. But there is a far more important difference in the circumstance, that in Spiders head and chest are united; and this corroborates the inferiority which an additional pair of legs ascribes to them among Insects. Spiders, indeed, should be considered as pupa-like Insects in a perfect state of development, not undergoing a further growth, but assuming, in that stage of progress, their final development as perfect animals. The greater resemblance of their jaws and antennæ to legs would also sustain this view.

As for the Myriapoda, we can consider them as caterpillar-like Insects, in which the respiratory organs, the masticatory organs, and the organs of locomotion, assume their final growth, under a worm-like form, and the whole body presents true entomological characters at a period of development when it still preserves the form of a larva with many joints, with legs upon all the joints, and the head only distinct from the other rings, but resembling Insects in their antennæ, in their compound eyes, in their articulated feet, in their stigmata, and in almost every detail of internal structure. This resemblance is even so close to the structure of some Coleoptera, that one is almost tempted to view the Brachelytra as a connecting link between this lower order of Insects and the Myriapoda. Fig. *h* of the foregoing wood-cut, which represents a species of *Polydesmus*, will show this analogy between Myriapoda and the larva of Insects, as well as with the Worms and lower Crustacea, and Fig. *g*, which represents a Spider, *Salticus scenicus*, will show the corresponding analogy between this group of Articulata and the pupa of Insects, as well as with the higher Crustacea. In the highest class of Articulata, including Myriapoda, Arach-

nidæ, and other Aptera, and true Insects, we have thus, with the organization of Insects proper, a repetition of the natural forms of the three classes of the type. We have worm-like Insects, the Myriapoda,—Crustacea-like Insects, the Spiders,—and true Insects, with wings, and six legs; or, in another point of view, larva-like Insects, Myriapoda,—pupa-like Insects, Spiders,—and true Insects, above all; the larval and worm-like condition being both expressed in the form of Myriapoda, while the pupa-like and Crustacea-like form is shown in the Spiders, and the true Insects, as the highest stage of development, rank above all. So that the special classification of Insects proper, again, sustains the general classification of Articulata, in which we have ascribed the lowest rank to Worms, the intermediate position to Crustacea, and the highest to Insects.

EXPLANATION OF THE PLATE.

Fig. 1. Egg of *Eudamus Tityrus*, natural size; Fig. 1^a, enlarged in profile; Fig. 1^b, enlarged from above; Fig. 1^c, a rib of the same egg still more enlarged.

Figs. 2, 3, 4, 5, and 6. Larvæ of *Eudamus Tityrus*, in different stages of growth.

Fig. 7. Pupa of the same; Fig. 7, the pupa in its loose cocoon, with the larva-skin cast at its side; Fig. 7^a, the pupa seen in profile; Fig. 7^b, the same seen from above.

Figs. 8, 9, and 10. The larva before casting its last skin.

Figs. 11, 12, and 13. The larva casting its last skin, and the pupa coming out; seen in profile, Fig. 11, from above, Fig. 12, and from below, Fig. 13.

Figs. 14, 15, 16. The pupa entirely detached from the larva-skin, which hangs behind the abdomen; Fig. 14, seen in profile; Fig. 15, from above; Fig. 16, from below. The wings, legs, antennæ, and trophi are entirely free.

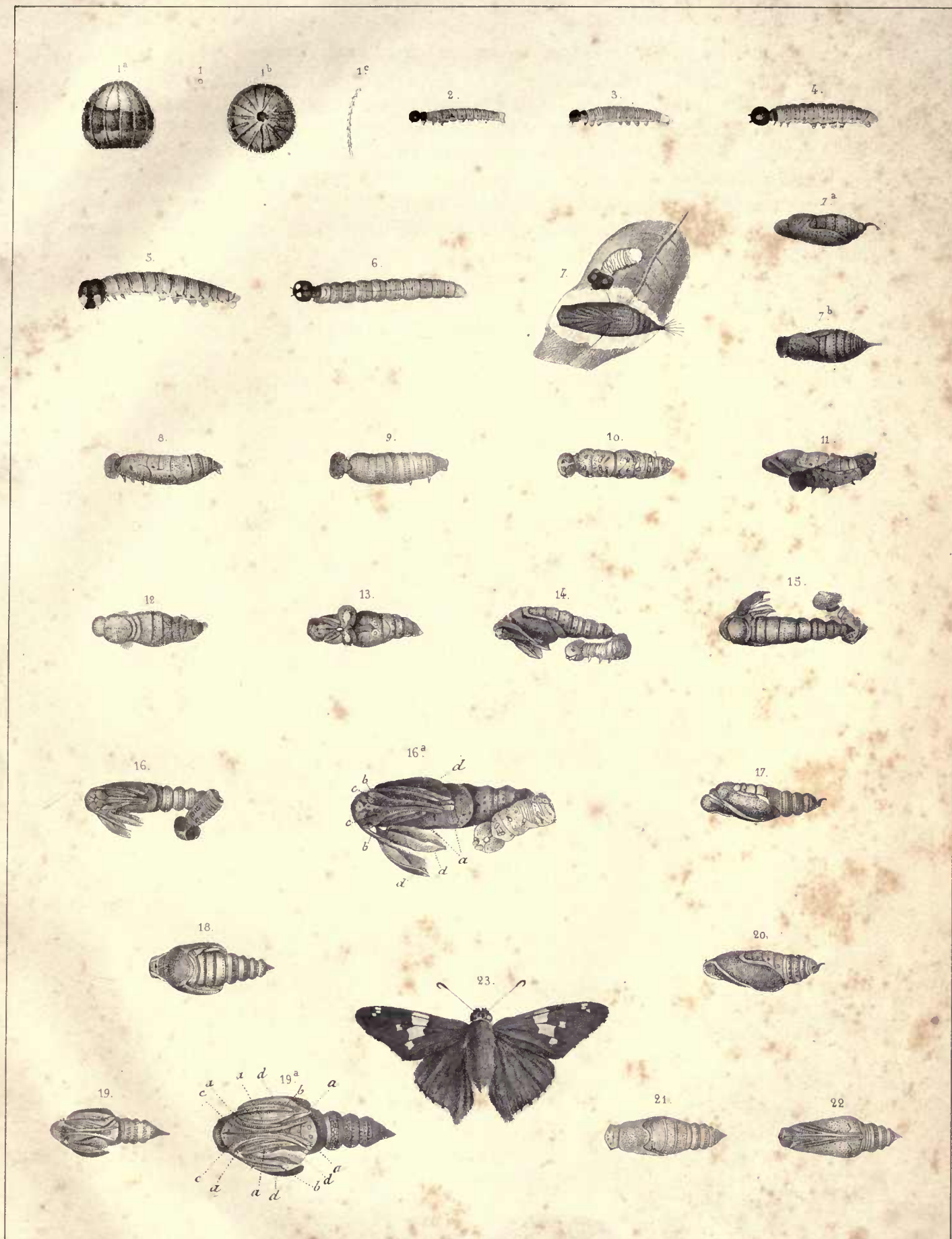
Fig. 16^a represents the same pupa as Fig. 16, somewhat enlarged; *d d* being the vesicular wings, *c c*, the jaws, *b b*, the antennæ, and *a*, the legs.

Figs. 17, 18, and 19 represent the pupa entirely freed from the larva-skin, and somewhat more advanced than in Figs. 14, 15, and 16; the wings, antennæ, and trophi being, however, still free.

Fig. 19^a represents the same pupa as Fig. 19, somewhat enlarged; *d d* being the vesicular wings, *c c*, the jaws, *b b*, the antennæ, and *a a a*, the legs.

Figs. 20, 21, and 22. The pupa nearly perfect; the wings being flattened upon the sides of the body, and beginning to adhere to the chest, as also to the antennæ, trophi, and legs. Fig. 20, seen from the side; Fig. 21, from above; Fig. 22, from below.

Fig. 23. *Eudamus Tityrus*, in its perfect state of development.



J. Burkhards from nat.

Tappan & Bradford's lith.

A. Sorel on stone

EUDAMUS TITYRUS.

299308		Q1468
Agassiz, L.J.R.		A5
The classification of insects		BIOLOGY LIBRARY
MAR 22 1929	Franklin	MAY 1 1929
JUL 5 1931		
Biology Library		
OCT 23 1931	C.E. Norland	OCT 17 1931
MAY 6 1933	Baker	MAY 21 1933
MAY 7 1941	Pine	MAY 13 1941

299308

Agassiz

A5

BIOLOGY LIBRARY

UNIVERSITY OF CALIFORNIA LIBRARY

THIS BOOK IS DUE ON THE LAST DATE
STAMPED BELOW

AN INITIAL FINE OF 25 CENTS
WILL BE ASSESSED FOR FAILURE TO RETURN
THIS BOOK ON THE DATE DUE. THE PENALTY
WILL INCREASE TO 50 CENTS ON THE FOURTH
DAY AND TO \$1.00 ON THE SEVENTH DAY
OVERDUE.

Biology Library

MAY 6 1933

MAY 7 1941

OCT 20 1948

DEC - 8 1948

LD 21-50m-1,'33

